

How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe

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Abstract Within a landscape where prey has an aggregated distribution, predators can take advantage of the spatial autocorrelation of prey density and intensify their search effort in areas of high prey density by using area-restricted search behaviour. In African arid and semi-arid savannas, large herbivores tend to aggregate around scarce water sources. We tested the hypothesis that water sources are a key determinant of habitat selection and movement patterns of large free-ranging predators in such savannas, using the example of the African lion. We used data from 19 GPS radio-collared lions in Hwange National Park, Zimbabwe. Maps of lions' trajectories showed that waterholes are key loci

on the lions' route-maps. Compositional analyses revealed that lions significantly selected for areas located within 2 km of a waterhole. In addition, analysis of lions' night paths showed that when lions are close to a waterhole (<2 km), they move at lower speed, cover shorter distances per night (both path length and net displacement) and follow a more tortuous path (higher turning angle, lower straightness index and higher fractal dimension) than when they are further from a waterhole. Hence, our results strongly suggest that lions adopt area-restricted searching in the vicinity of waterholes, and reduce their search effort to minimize the time spent far from a waterhole. They provide an illustration of how key habitat features that determine the dispersion of prey (e.g. waterholes in this study) have an influence on the spatial ecology and movement patterns of terrestrial predators.

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Introduction

Landscapes are characterized by spatial heterogeneity (Kotliar and Wiens 1990) and the interaction between animal movement and landscape structure is a key process in a large spectrum of fundamental behavioural and ecological processes such as foraging behaviour

(e.g. Etzenhouser et al. 1998; Bailey and Thompson 2006), spatial distribution of animals (Turchin 1991), migration and dispersal (Gustafson and Gardner 1996). The characteristics of an animal's movements reflect its relationships with diverse abiotic and biotic factors and may be influenced by habitat characteristics (e.g. Bélisle et al. 2001), resource abundance and distribution (Fauchald 1999), predation risk (e.g. Fortin et al. 2005; Frair et al. 2005), and other complex behavioural processes (e.g. Roshier et al. 2008). However, it is commonly accepted that, all else being equal, animals should spend more time, and move differently, in areas where resources are abundant than in areas where they are scarce.

Within a landscape where prey has an aggregated distribution, predators can take advantage of the spatial autocorrelation of prey density and intensify their search effort in areas of high prey density by using area-restricted search behaviour, i.e. lowering speed and increasing turning rate in response to increased resource abundance (Smith 1974a, b; Kareiva and Odell 1987). In areas of lower prey density, an extensive search mode is expected, where rapid, straight-line travel minimizes the time spent between rich patches and reduces search effort (Zollner and Lima 1999). Besides, animals can use their navigation capacity, i.e. their ability to choose a heading destination and know their location relative to their destination, to adopt oriented movement and travel by orienting themselves towards a given goal (Nams 2006). This is very likely to be the case when patches of resources are clearly identified in the landscape. Consequently, perception of prey abundance and distribution can dictate directly which mode of search behaviour is employed, and may have an important effect on the movement patterns of predators. The development of radio- and satellite-telemetry now facilitates a finer understanding of how animals travel at large spatial or temporal scales and the recent combined use of such data with Geographic Information System (GIS) has become a powerful tool to investigate the interaction between animal movement and their environment. The relationship between search patterns and the distribution of prey has been documented for large free-ranging predators in marine ecosystems (e.g. Pinaud and Weimerskirch 2005; Bailey and Thompson 2006) but extremely little is known for large free-ranging

predators in terrestrial ecosystems (but see Atkinson et al. 2002).

Animal movement has been the focus of much theoretical and empirical work over the past 25 years, and the methods used have been very diverse including correlated random walk (Kareiva and Shigesada 1983), fractal analysis (With 1994; Nams 2005; e.g. Fritz et al. 2003), first passage time (Fauchald and Tveraa 2003), Lévy flights (Viswanathan et al. 1996), and state-space models (Jonsen et al. 2003). Often, the approaches are aimed at (1) determining the scale at which the animal uses area-restricted search behaviour, (2) identifying the areas where the animal uses area-restricted search behaviour and ultimately (3) assessing the habitat variables that characterizes such areas (e.g. Pinaud and Weimerskirch 2005). Here we propose a new hypothesis-testing approach. In arid and semi-arid savannas, large herbivores tend to aggregate around scarce water sources (Thrash et al. 1995; Redfern et al. 2003). Hence, we tested the hypothesis that water sources are a key determinant of movement patterns of large carnivores in arid and semi-arid savannas. In particular, predators should adopt area-restricted search behaviour in areas located in the vicinity of a waterhole, where their encounter rate with potential prey is very likely to be higher.

We used data from 19 GPS radio-collared African lions (*Panthera leo*) in Hwange National Park, Zimbabwe, where ungulate habitat selection is strongly influenced by the distance to waterholes (Valeix et al. 2009). We tested the hypotheses that (1) waterholes attract lions resulting in selection for habitats in the vicinity of waterholes, and (2) lion movement characteristics are influenced by the distance to a waterhole. More particularly, we tested whether lions show area-restricted search behaviour in the vicinity of waterholes (characterized by increased turning rate and lower speed) and move faster and in straighter lines further from waterholes. In addition, we hypothesize that seasonality in semi-arid systems has an important effect on lion movement patterns with waterholes having a greater influence on lion movements under drier conditions (with area-restricted search being more pronounced as the dry season progresses) since prey are expected to be more aggregated around waterholes when water sources are scarcer.

Methods

Study site and animals

The study was carried out in the northern part of Hwange National Park (HNP). HNP covers c. 15,000 km² of dystrophic savanna in north-western Zimbabwe (19°00' S, 26°30' E). Altitude varies from 800 to 1100 m. The vegetation is primarily woodland and bushland savanna (64%) and vegetation communities are dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). HNP is a semi-arid ecosystem with a mean annual rainfall of 606 mm and where annual rainfall is highly variable (CV \approx 30%). Most rain falls between November and February. Three seasons are distinguished in this study: wet season (November–February), early dry season (March–June) and late dry season (July–October). The surface water available to animals is largely dependent on rainwater collected in natural depressions that are generally dry at the end of the dry season, and artificial permanent dams or waterholes, which are pumped during the dry season (~55 waterholes). A GIS layer of all main waterholes (all pumped waterholes and the largest natural ones that retain water throughout the dry season in most years) was available.

Since 2002, lions were closely monitored in the study area, of which 11 female and 8 male adults were fitted with GPS Simplex radio-collars (female: 900 g, male: 950 g; Televilt Positioning AB, Lindesberg, Sweden; see Loveridge et al. 2007 for details) and provided regular and continuous data over long periods. For each animal, one location was available hourly from 1800 to 700 hours. We extracted the distance to the closest waterhole for each location using ESRI ArcMap 9.2.

Site selection analyses

We performed compositional analyses (Aebischer et al. 1993), a method that uses individuals as sampling units, using the package “adehabitat” for R software (Calenge 2006) to examine whether lions preferentially used areas close to waterholes. Distance to water was categorized into five classes: 0–2, 2–4, 4–6, 6–8 and >8 km. For each animal, we calculated the proportion of locations within each distance-to-water

class (representative of site use) and the proportion of each distance-to-water class in the animal’s home range (representative of site availability). Home ranges were calculated using the 95% probability contour of all locations distribution using the kernel density estimator, a method with recognized strengths (Worton 1989; Powell 2000), and the reference smoothing factor h_{ref} (recommended by Hemson et al. 2005; Börger et al. 2006). Home range analyses were undertaken using Ranges 7 software (South and Kenward 2006). Site preferences were represented by the Manly-Chesson selection index (Manly et al. 1972; Chesson 1978), which is the proportional use divided by the proportional availability of distance-to-water class. This index value is <1 or >1 if the area is, respectively avoided or selected.

Night path characteristics

Because lions are largely nocturnal and their activity peaks are after 1700 hours and before 0800 hours (Schaller 1972), and our data are continuous (one location every hour) between 1800 and 700 hours the following morning, we considered the night path (as defined below) as the scale of interest. We defined the straight-line segment linking two successive locations taken at 1 h intervals as the step, and the combination of all steps from one night (from 1800 to 700 hours) as the sampling unit for the night path. Only nights for which all locations were available were used in the analyses of path characteristics (Table 1).

We used Hawth’s tools for ESRI ArcMap 9.2 (Beyer 2007) to extract movement characteristics (SL = step length (m), θ = turning angle (°)) between two consecutive locations (1 h), and we then calculated the following night path characteristics:

PL = total path length travelled per night (m).

ND = net displacement = distance between the starting and ending points of the night path (m).

S = Speed. It was either equal to SL when considering step length as one step length corresponds to 1 h or proportional to PL as one night corresponds to 13 h, hence $S = PL/13$ (m/h).

The tortuosity (i.e. the convoluted aspect) of an animal’s path is a key parameter which integrates distances travelled and turning angles and provides further information on how the animal has covered an area. We calculated two indices of tortuosity:

Table 1 Number of nights for which all locations (every hour from 1800 to 0700 hours) were available for each marked individual lion in Hwange National Park, Zimbabwe

| Year | Month | Females | | | | | | | | | | | | Males | | | | | | | | | | | |
|-----------|-----------|---------|----|----|----|----|----|----|-----|-----|-----|-----|----|-------|----|----|----|----|----|-----|----|----|--|--|--|
| | | F1 | F4 | F5 | F6 | F7 | F8 | F9 | F11 | F14 | F15 | F16 | M1 | M2 | M4 | M5 | M6 | M7 | M9 | M11 | | | | | |
| 2002 | June | | | | | | | | | | | | | | | | | | | | 17 | | | | |
| | July | | | | | | | | | | | | | | | | | | | | | 30 | | | |
| | August | | | | | | | | | | | | | | | | | | | | | 30 | | | |
| | September | | | | | | | | | | | | | | | 15 | 27 | | | | | 16 | | | |
| | October | | | | | | | | | | | | | | | 27 | 30 | | | | | 24 | | | |
| | November | | | | | | | | | | | | | | | 28 | 24 | | | | | 27 | | | |
| | December | | | | | | | | | | | | | | | 25 | 29 | | | | | 26 | | | |
| | January | | | | | | | | | | | | | | | 23 | 29 | | | | | 27 | | | |
| | February | 3 | 2 | | | | | | | | | | | | | 21 | 26 | | | | | 13 | | | |
| | March | 22 | 20 | | | | | | | | | | | | | 30 | 27 | | | | | | | | |
| | April | 12 | 25 | | 19 | | | | | | | | | | | 28 | 30 | | | | | | | | |
| | May | 21 | 16 | 12 | 28 | 9 | 21 | | | | | | | | | 31 | 10 | | | | | 9 | | | |
| June | 22 | 11 | 30 | 27 | 27 | 24 | | | | | | | | | 26 | 28 | | | | | 30 | | | | |
| July | 24 | 14 | 26 | 28 | 29 | 29 | | | | | | | | | 29 | 29 | | | | | 30 | | | | |
| August | 23 | 18 | 28 | 26 | 30 | 31 | 21 | | | | | | | | 14 | 22 | | | | | 28 | | | | |
| September | 22 | 20 | 29 | 26 | 29 | 26 | 25 | 5 | | | | | | | 28 | 27 | | | | | 27 | | | | |
| October | 20 | 22 | 30 | 30 | 30 | 29 | 29 | 30 | | | | | | | 25 | 31 | | | | | 25 | | | | |
| November | 23 | 18 | 30 | 27 | 29 | 29 | 30 | 27 | | | | | | | 26 | 28 | | | | | 30 | | | | |
| December | 14 | 18 | 28 | 27 | 26 | 31 | 25 | 25 | | | | | | | 28 | 29 | | | | | 26 | | | | |
| January | 7 | 16 | 23 | 27 | 26 | 25 | 24 | 14 | | | | | | | 28 | 30 | | | | | 28 | | | | |
| February | 4 | 15 | 23 | 26 | 19 | 16 | 24 | 19 | | | | | | | 25 | 27 | | | | | 25 | | | | |
| March | | 18 | 24 | 23 | 18 | 17 | 22 | 22 | | | | | | | 21 | 21 | | | | | 3 | | | | |
| April | | 24 | 26 | 23 | 24 | 25 | 21 | 24 | | | | | | | 16 | 16 | | | | | 14 | | | | |
| May | | 12 | 26 | 28 | 25 | 25 | 28 | 21 | | | | | | | 27 | 27 | | | | | 19 | | | | |
| June | | | 25 | 23 | 22 | 26 | 28 | 14 | | | | | | | 27 | 30 | | | | | 24 | | | | |
| July | | 15 | 28 | | 28 | 30 | 28 | 21 | | | | | | | 29 | 30 | | | | | 28 | | | | |
| August | | 19 | 22 | | 11 | 30 | 30 | 25 | | | | | | | 30 | 30 | | | | | 19 | | | | |
| September | | 21 | 25 | | 20 | 28 | 24 | 23 | | | | | | | 28 | 28 | | | | | 26 | | | | |
| October | | 27 | 26 | | 15 | 22 | 23 | 12 | | | | | | | 16 | 16 | | | | | 30 | | | | |
| November | | 20 | 28 | | 21 | 19 | 13 | | | | | | | | 28 | 15 | | | | | 29 | | | | |
| December | | 15 | 30 | | 16 | 17 | | | | | | | | | 28 | 3 | | | | | 16 | | | | |
| | | | | | | | | | | | | | | | 25 | 25 | | | | | 25 | | | | |

Table 1 continued

| Year | Month | Females | | | | | | | | | | | Males | | | | | | | | | | |
|------|-----------|---------|----|----|----|----|----|----|-----|-----|-----|-----|-------|----|----|----|----|----|----|-----|--|--|--|
| | | F1 | F4 | F5 | F6 | F7 | F8 | F9 | F11 | F14 | F15 | F16 | M1 | M2 | M4 | M5 | M6 | M7 | M9 | M11 | | | |
| 2005 | January | 8 | | 30 | | 5 | 5 | | 4 | 30 | 3 | 2 | | | | | 8 | | | | | | |
| | February | 13 | | 24 | | 5 | | 25 | 24 | 3 | | | | | | | | | | | | | |
| | March | 13 | | 13 | | 3 | | 29 | 25 | 2 | | | | | | | | | | | | | |
| | April | 13 | | | | 4 | | 1 | 28 | 20 | | | | | | | | | | | | | |
| | May | 26 | | | | 8 | | | 25 | 18 | | | | | | | | | | | | | |
| | June | 20 | | | | 6 | | | 28 | 20 | | | | | | | | | | | | | |
| | July | 22 | | | | 11 | | | 30 | 20 | | | | | | | | | | | | | |
| | August | 22 | | | | 11 | | | 30 | 18 | | | | | | | | | | | | | |
| | September | 20 | | | | 16 | | | 29 | 18 | | | | | | | | | | | | | |
| | October | 11 | | | | 8 | | | 31 | 20 | | | | | | | | | | | | | |
| | November | | | | | 3 | | 27 | 29 | 20 | | | | | | | | | | | | | |
| | December | 7 | | | | | | 30 | 10 | 23 | | | | | | | | | | | | | |
| 2006 | January | 12 | | | | | 30 | 1 | 25 | 1 | | | | | | | | | | | | | |
| | February | 5 | | | | | 21 | 17 | 18 | | | | | | | | | | | | | | |
| | March | 8 | | | | | 23 | 15 | 20 | | | | | | | | | | | | | | |
| | April | 16 | | | | | 20 | 15 | 27 | | | | | | | | | | | | | | |
| | May | 14 | | | | | 30 | 21 | 27 | | | | | | | | | | | | | | |
| | June | 4 | | | | | 27 | 28 | 28 | | | | | | | | | | | | | | |
| | July | 2 | | | | | 23 | 28 | 23 | | | | | | | | | | | | | | |
| | August | | | | | | 26 | 1 | 31 | 27 | | | | | | | | | | | | | |
| | September | | | | | | 24 | 3 | 27 | 18 | | | | | | | | | | | | | |
| | October | | | | | | 29 | 1 | 29 | | | | | | | | | | | | | | |
| | November | | | | | | 28 | | 27 | | | | | | | | | | | | | | |
| | December | | | | | | 26 | | 6 | | | | | | | | | | | | | | |
| 2007 | January | | | | | | 26 | | 26 | | | | | | | | | | | | | | |
| | February | | | | | | 23 | | 21 | | | | | | | | | | | | | | |
| | March | | | | | | 21 | | 16 | | | | | | | | | | | | | | |
| | April | | | | | | | 15 | | | | | | | | | | | | | | | |
| | May | | | | | | | 18 | 8 | | | | | | | | | | | | | | |
| | June | | | | | | | 21 | 2 | | | | | | | | | | | | | | |
| | July | | | | | | | 5 | | | | | | | | | | | | | | | |

Table 1 continued

| Year | Month | Males | | | | | | | | | | | | | | | | | | |
|------|-----------|---------|----|----|----|----|----|-------|-----|-----|-----|-----|----|----|----|----|----|----|----|-----|
| | | Females | | | | | | Males | | | | | | | | | | | | |
| | | F1 | F4 | F5 | F6 | F7 | F8 | F9 | F11 | F14 | F15 | F16 | M1 | M2 | M4 | M5 | M6 | M7 | M9 | M11 |
| | August | | | | | | | | | 28 | 11 | | 13 | | | | | | | |
| | September | | | | | | | | | 28 | | | 19 | | | | | | | |
| | October | | | | | | | | | 31 | | | 15 | | | | | | | |
| | November | | | | | | | | | 13 | | | 4 | | | | | | | |

SI = straightness index = ND/PL (Batschelet 1981). SI ranges between 0 (very convoluted path) and 1 (straight line).

D = fractal mean dimension developed by Nams (Nams 2005; available at <http://www.nsac.ns.ca/envsci/staff/vnams/fractal.htm>). D ranges between 1 (straight line) and 2 (path is so tortuous as to cover a plane).

SI and D are different measures of path tortuosity which are not redundant and capture different characteristics of trajectories. Whereas SI tend to capture the straightness of a path, D captures how well the potential area within which the path is located is covered by the animal (Fig. 1).

We predicted that in the vicinity of waterholes SL and PL should be smaller (i.e. S should be smaller), θ should be higher, ND should be smaller, and that the tortuosity of the path should be higher (i.e. SI smaller and D higher) than in areas far from a waterhole.

Analysis of night path characteristics

For the following analyses, we divided the landscape into 3 classes of distance to water: 0–2 km (close), 2–6 km (intermediate), and 6–10 km (far). Because males and females are likely to exhibit different

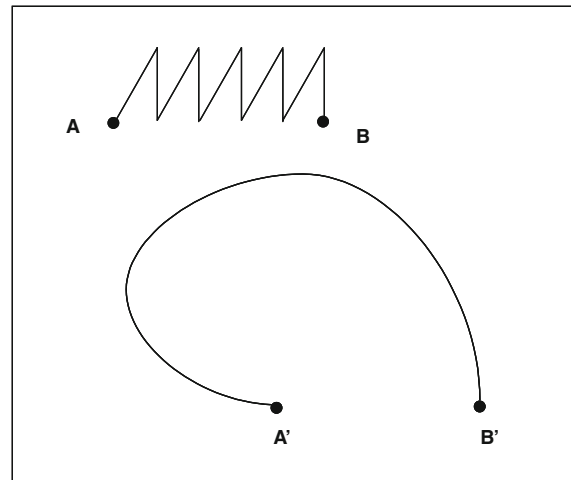


Fig. 1 This figure illustrates how different tortuosity measures may measure different aspects of a trajectory. For the same net displacement, an animal may choose to move following a path of type A–B or of type A'–B'. Even though the straightness index may be very similar in the 2 situations, the fractal dimension will be significantly higher for the path of type A–B than for the path of type A'–B'

spatial behaviour, data gathered on males and females were analysed separately. We performed 2 sets of analyses. (a) We first performed a covariance analysis on step characteristics (SL (i.e. S) and θ) with lion identity and night identity as random effects and with two fixed class variables: distance-to-water and season. We also tested the interaction between distance-to-water and season as we expected the differences between movements characteristics to be higher in the late dry season than in the early dry season and in the wet season. For analysis of θ , we considered the absolute values of turning angles, hence turning angles ranged from 0° to 180° and we used linear statistics in analysis of turning angles. As temporal serial autocorrelation may affect the data from a same night, we checked whether autocorrelation was present and accounted for it using a first-order autoregressive covariance structure. (b) Then, each night path was assigned to one of the 3 classes of distance to water (if all locations belonged to one class) or removed from the analyses when it covered several classes (e.g. a night path starting close to a waterhole and finishing at 8 km from a waterhole). This allowed us to compare night paths in contrasted areas of the landscape. To rigorously test our hypotheses, we also needed to avoid any bias linked to the surface and/or edge effect due to our landscape sampling design. Because ND in the 0–2 km class from a waterhole are likely to be smaller than ND in the other classes (the maximum distance between two points in the 0–2 km class is 4 km whereas it can be as long as 12 km in the 2–6 km class and 20 km in the 6–10 km class), we considered night paths with $ND \leq 4$ km only in the following analyses (see also Appendix—electronic supplementary material). We performed a covariance analysis on each night path characteristic (PL (i.e. S), ND, SI and D) with lion identity as random effect and with distance-to-water, season, and the interaction between both as fixed effects. Statistical analyses were performed with SAS software (version 8.2), using MIXED procedure.

Results

The mapping of lion trajectories clearly showed that waterholes play a key role in shaping movement patterns and influencing lion spatial ecology (Fig. 2).

Site selection

Lions of both sexes showed significant selection for sites located within 2 km of a waterhole (female_{all seasons}: $\lambda = 0.148$, $P = 0.002$; male_{all seasons}: $\lambda = 0.027$, $P = 0.012$; Table 2). The pattern of selection was similar for all seasons (Fig. 3) with both sexes significantly selecting for areas located within 2 km of a waterhole during each season (all $P < 0.05$) except for females in the early dry season for which site selection fell just short of significance (female_{early dry season}: $\lambda = 0.315$, $P = 0.064$).

Night path characteristics

Characteristics of lion movement appeared to differ in the different classes of distance to a waterhole (Table 3).

Influence of the interaction between distance-to-water and season

For females, the interaction between distance-to-water and season had no significant influence on night path characteristics (all $P > 0.05$). However, both season and distance-to-water independently influenced night path characteristics, with distance-to-water having the most significant effect (Fig. 4; Table 4; see below for more details). For males, this interaction influenced path length (Table 5) with the most pronounced differences in the late dry season (Fig. 5c).

Influence of distance-to-water

Lions of both sexes moved significantly slower in areas close to a waterhole (Tables 4 and 5; Figs. 4a and 5a). On average, female lions travelled 20% quicker when they were far from a waterhole than when they were close, and male lions more than 50% quicker (Table 3). The mean path length travelled by a female lion per night and the net displacement were significantly longer in areas far and at intermediate distances from a waterhole than in areas close to a waterhole (Table 4; Fig. 4c and d). On average, female lions travelled ~ 1.5 km more per night when they were far from a waterhole than when they were close, and covered a net displacement approximately one-third longer (Table 3). For males, the difference

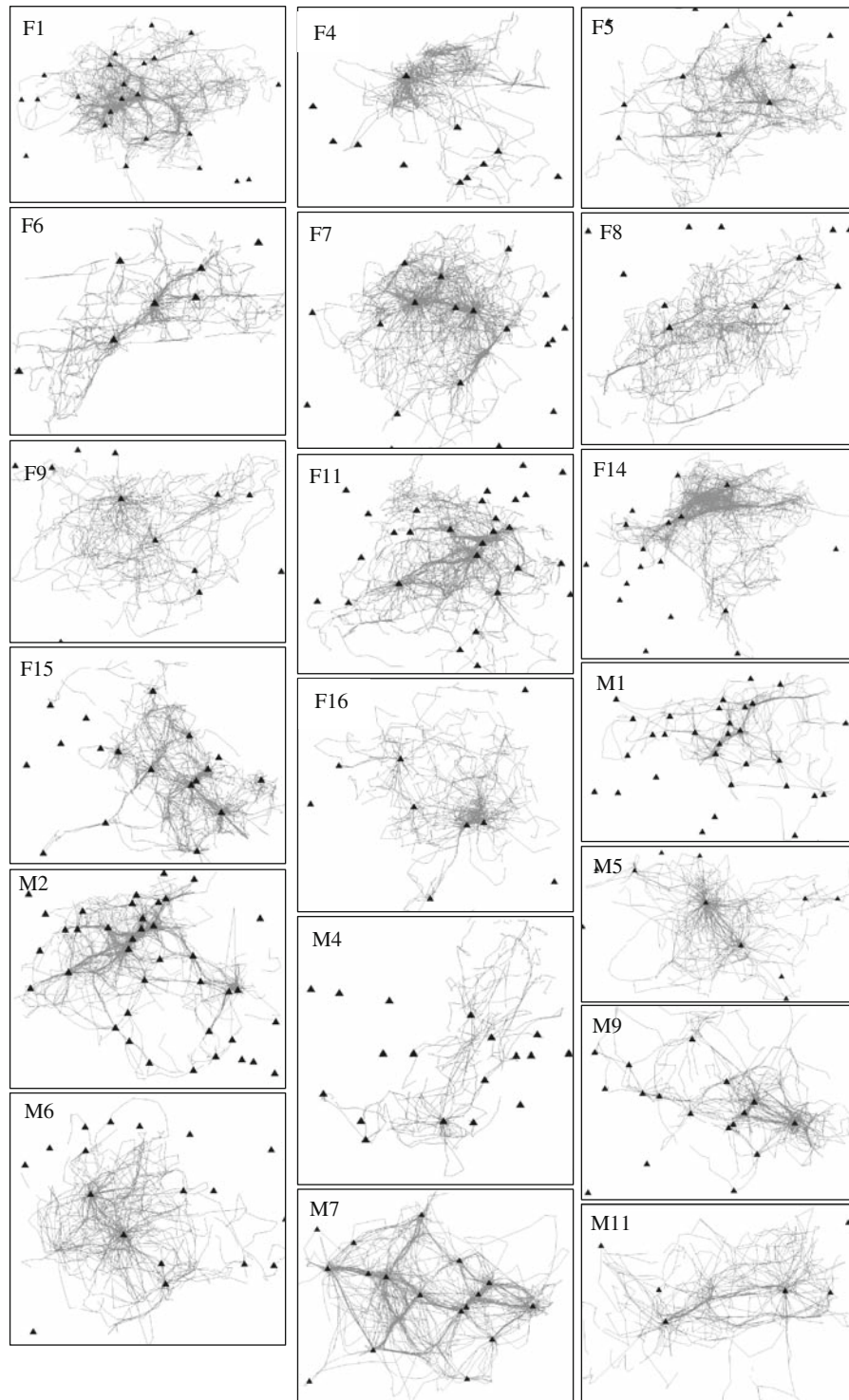


Fig. 2 Maps showing trajectories for each study lion (e.g. F1 is the map for female 1, M1 is the map for male 1). *Black triangle* symbols represent main waterholes in the study area

Table 2 Site selection at different distances from water for lions in Hwange National Park, Zimbabwe

| | 0–2 km | 2–4 km | 4–6 km | 6–8 km | >8 km |
|----------------|--------|--------|--------|--------|-------|
| Females | | | | | |
| 0–2 km | 0 | +++ | +++ | +++ | +++ |
| 2–4 km | --- | 0 | +++ | + | + |
| 4–6 km | --- | --- | 0 | + | + |
| 6–8 km | --- | - | - | 0 | + |
| >8 km | --- | - | - | - | 0 |
| Males | | | | | |
| 0–2 km | 0 | +++ | +++ | +++ | +++ |
| 2–4 km | --- | 0 | + | + | - |
| 4–6 km | --- | - | 0 | + | - |
| 6–8 km | --- | - | - | 0 | - |
| >8 km | --- | + | + | + | 0 |

The results presented are from a compositional analysis. At the intersection of a row and a column, there is a “+” when the row class is more used than the column class, and “-” otherwise. When the difference is significant, the sign is tripled

in path length only held in the late dry season (Fig. 5c) and net displacement was significantly different only between the 0–2 km and 2–6 km distance-to-water classes (Table 5; Fig. 5d—it is likely that there was no difference with the 6–10 km class because of the wet season pattern only). Mean turning angle was significantly higher in areas close to a waterhole than in other areas for both sexes (Tables 4 and 5). Lions appeared to have a tendency to move straighter (lower mean turning angle) when they were not close to a waterhole, and this pattern was consistent across seasons, but the differences in mean turning angle were not large (Table 3; Figs. 4b and 5b). This is consistent with results for tortuosity. First, for females the straightness index was significantly lower, i.e. indicated a more convoluted path, in areas close to a waterhole than in areas at intermediate distances and far from a waterhole (Table 4; Fig. 4e). Second, the fractal dimension of lion night paths was significantly higher, i.e. also indicated a more convoluted path, in areas close to a waterhole for both sexes (Tables 4 and 5; Figs. 4f and 5f).

Influence of season

Season did not strongly influence night path characteristics. However, females showed a significantly

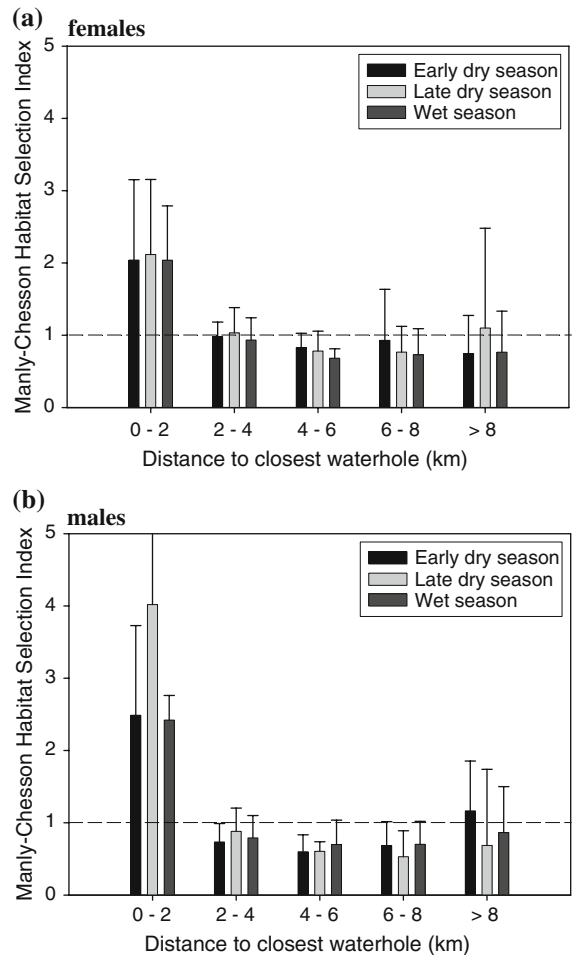


Fig. 3 Manly-Chesson selection index for each distance-to-water class and each season for (a) females and (b) males. Values above 1 indicate preference, values below 1 indicate avoidance and values equal to 1 indicate use in proportion of availability. Error bars represent the standard errors

higher straightness index, i.e. indicated a straighter path, in the early dry season (Table 4; Fig. 4e). Additionally, males covered larger net displacement per night in the early dry season (Table 5; Fig. 5d).

Discussion

First, our results clearly show that waterholes are key loci on the lions’ route-maps and that lions make use of several waterholes (see Fig. 2). They may need to monopolise a sufficient number of waterholes to rotate their hunting areas between several to avoid prey predicting their whereabouts. Our results also

Table 3 Estimate \pm SE of night path movement characteristics for African lions in Hwange National Park, Zimbabwe, at different distances from water

| | Distance to a waterhole | | | Distance to a waterhole | | |
|---------------------------------------|-------------------------|-----------------|-----------------|-------------------------|-----------------|-----------------|
| | Females | | | Males | | |
| | 0–2 km | 2–6 km | 6–10 km | 0–2 km | 2–6 km | 6–10 km |
| Step length SL (m) or speed S (m/h) | 518 \pm 14 | 611 \pm 12 | 625 \pm 27 | 623 \pm 25 | 955 \pm 24 | 952 \pm 52 |
| Turning angle θ ($^\circ$) | 75 \pm 1 | 72 \pm 1 | 73 \pm 2 | 72 \pm 1 | 60 \pm 1 | 62 \pm 2 |
| Path length PL (m) | 3773 \pm 373 | 5074 \pm 342 | 5369 \pm 386 | 3367 \pm 497 | 3881 \pm 558 | 4143 \pm 504 |
| Net displacement ND (m) | 1425 \pm 124 | 1971 \pm 114 | 1936 \pm 123 | 1392 \pm 181 | 1720 \pm 207 | 1531 \pm 182 |
| Straightness index SI | 0.41 \pm 0.03 | 0.48 \pm 0.03 | 0.46 \pm 0.03 | 0.45 \pm 0.05 | 0.50 \pm 0.05 | 0.48 \pm 0.05 |
| Fractal dimension D | 1.10 \pm 0.01 | 1.08 \pm 0.01 | 1.07 \pm 0.01 | 1.11 \pm 0.01 | 1.09 \pm 0.01 | 1.09 \pm 0.01 |

clearly show that waterholes are a key determinant of lion habitat selection in arid and semi-arid savannas, such as HNP, where water sources are scarce and patchily distributed. Because the distribution of herbivores in such ecosystems is largely influenced by the distribution of surface water (Redfern et al. 2003; Valeix et al. 2009), lions have a greater chance of encountering their prey in areas surrounding waterholes, and our results showed that lions tend to spend most time in such areas. Our results are therefore consistent with the idea that animals should spend more time in areas where resources are plentiful than in areas where they are scarce. Water sources have already been considered as crucial in lion habitat selection in the Serengeti (Mosser 2008). Through their influence on habitat selection, waterholes are likely to affect both lion home range size and configuration. This is the case in HNP where Loveridge et al. (2009) showed that home range size is partly determined by the density of waterholes, suggesting that the dispersion of waterholes across the landscape determines potential lion territories.

Second, our results indicate that lions of both sexes adopt different movement patterns in areas close to and far from waterholes. The results are clear-cut for female lions and consistently distinguish night path characteristics between areas close to waterholes (<2 km) and those further afield. Male lions also showed different movement patterns in these two categories of areas, but the statistical significance of these differences is less consistent than for females, probably owing to the males' need to patrol their home ranges. When lions are close to a waterhole

(<2 km), they move at lower speed, cover shorter distances (both path length and net displacement) and follow a more tortuous path (higher turning angle, lower straightness index and higher fractal dimension) than when they are further from a waterhole. This may indicate that, by lowering their speed and increasing their turning rate, lions tend to concentrate their search activity in areas surrounding waterholes, i.e. of potential high prey density. In short, our results strongly suggest that lions adopt area-restricted search patterns in the vicinity of waterholes. When lions are far from a waterhole (>6 km), our results show that they adopt rapid and more straight line movements. This may indicate that they reduce their search effort and tend to minimize the time spent far from a waterhole, i.e. in areas of lower prey density. This is consistent with an extensive search mode between rich patches (Zollner and Lima 1999). The dramatically biased distributions of lion locations (see Fig. 2) may not be solely explained in the framework of area-restricted search behaviour. Navigation capacity (the ability of animals to orient and navigate), which has been under-studied in movement models (Holyoak et al. 2008), may also greatly contribute to the web-like pattern shown (Fig. 2). The tendency for directed movements by lions to waterholes may, together with more convoluted paths in the vicinity of waterholes, be key in understanding the spatial patterns of lion behaviour.

Prey are expected to be crowded around a very small number of waterholes in the late dry season and to be more homogeneously dispersed in the wet season. Hence, we expected lions to (1) adopt contrasting movement patterns in the late dry season,

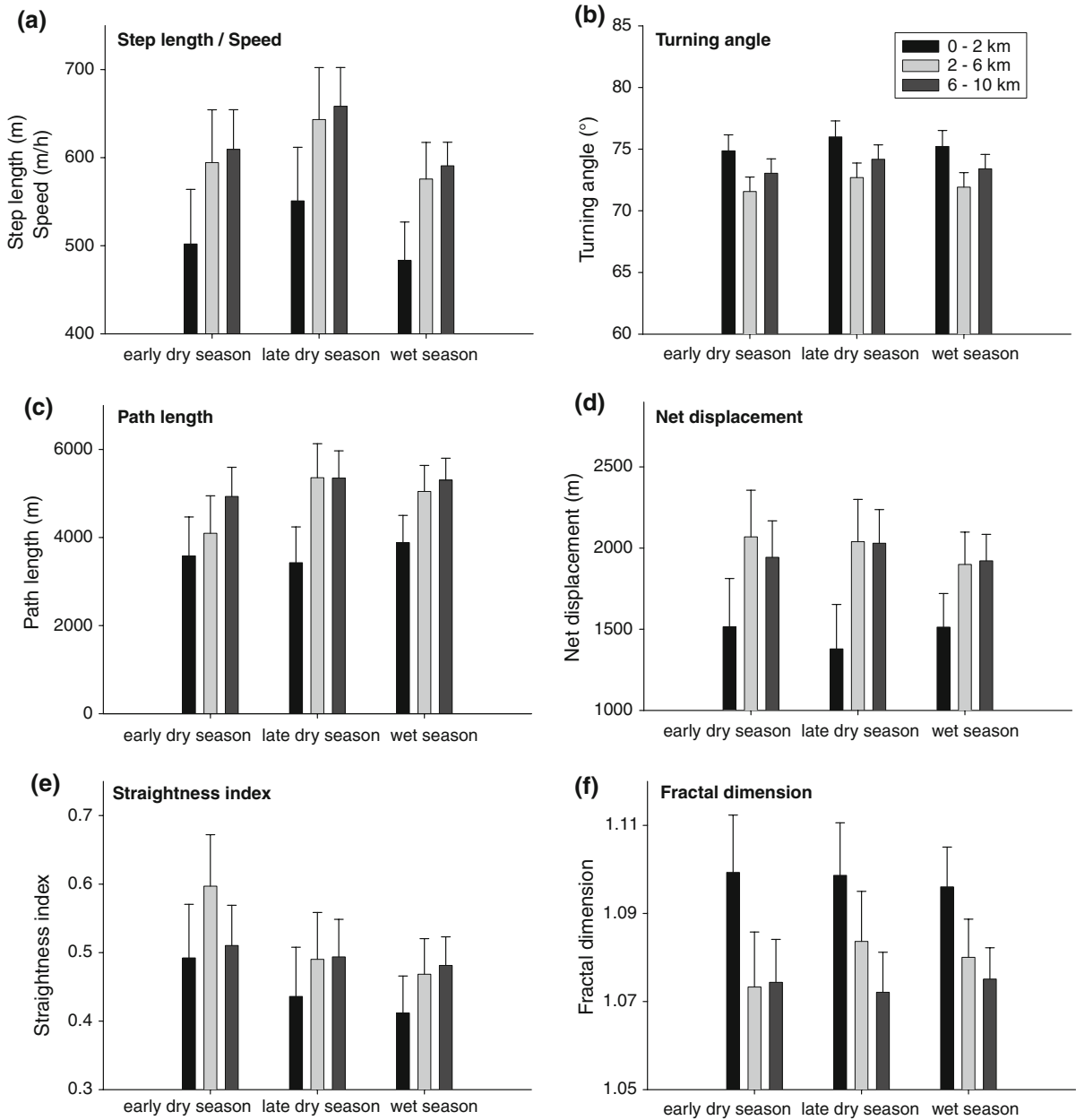


Fig. 4 Representation of female African lions night path movement characteristics (estimate + SE) for each distance-to-water class and each season in Hwange National Park, Zimbabwe. The following night path characteristics are

with area-restricted search behaviour close to waterholes and extensive search mode when far from them, and (2) adopt a more homogeneous movement pattern in the wet season, when prey are more dispersed. However, the interaction between season and distance-to-water did not play a significant role in lion

displayed: **a** step length (it also equals speed since step length is the distance travelled during 1 h), **b** turning angle, **c** path length, **d** net displacement, **e** straightness index, and **f** fractal dimension

habitat selection and for most lion night path characteristics. But seasonality did play some role in lion movement patterns. Interestingly, the straightness index for females was significantly higher (i.e. indicating a straighter path) in the early dry season, and males had larger net displacements per night in

Table 4 Summary statistics for mixed models of night path movement characteristics for female African lions in Hwange National Park, Zimbabwe

| | Variables | <i>df</i> | <i>F</i> | <i>P</i> | |
|----------------------------|-------------------|-----------|----------|----------|--------------------|
| Step length SL (m) or | Season | 2, 30380 | 8.66 | 0.0002 | Late > early & wet |
| Speed <i>S</i> (m/h) | Distance-to-water | 2, 30380 | 34.09 | <0.0001 | I < II & III |
| Turning angle θ (°) | Season | 2, 24771 | 0.48 | 0.6178 | |
| | Distance-to-water | 2, 24771 | 6.22 | 0.0020 | I > II & III |
| Path length PL (m) | Season | 2, 615 | 2.17 | 0.1152 | |
| | Distance-to-water | 2, 615 | 12.24 | <0.0001 | I < II & III |
| Net displacement ND (m) | Season | 2, 615 | 0.21 | 0.8084 | |
| | Distance-to-water | 2, 615 | 15.87 | <0.0001 | I < II & III |
| Straightness index SI | Season | 2, 615 | 4.77 | 0.0088 | Early > late & wet |
| | Distance-to-water | 2, 615 | 3.44 | 0.0327 | I < II & III |
| Fractal dimension <i>D</i> | Season | 2, 615 | 0.35 | 0.7059 | |
| | Distance-to-water | 2, 615 | 12.37 | <0.0001 | I > II & III |

The last column provides qualitative information on the results, with symbols indicating significance between classes at the *P* level of 0.05. I, II and III represent the 3 classes of distance to water: 0–2 km (close), 2–6 km (intermediate), and 6–10 km (far), respectively. Early, late and dry represent the early dry season, the late dry season and the wet season, respectively. See Fig. 4 for the graphical representation of the results. The interaction season*distance-to-water is not represented in this table because its effect was non significant at the *P* level of 0.05 for all night path characteristics

Table 5 Summary statistics for mixed models of night path movement characteristics for male African lions in Hwange National Park, Zimbabwe

| | Variables | <i>df</i> | <i>F</i> | <i>P</i> | |
|----------------------------|-------------------|-----------|----------|----------|--------------------|
| Step Length SL (m) or | Season | 2, 22759 | 2.17 | 0.1139 | |
| Speed <i>S</i> (m/h) | Distance-to-water | 2, 22759 | 180.49 | <0.0001 | I < II & III |
| Turning angle θ (°) | Season | 2, 18864 | 1.79 | 0.1673 | |
| | Distance-to-water | 2, 18864 | 64.26 | <0.0001 | I > II & III |
| Path length PL (m) | Season | 2, 322 | 1.89 | 0.1535 | |
| | Distance-to-water | 2, 322 | 3.35 | 0.0364 | |
| | Interaction | 4, 322 | 2.40 | 0.0501 | See Fig. 5 |
| Net displacement ND (m) | Season | 2, 326 | 5.05 | 0.0069 | Early > late & dry |
| | Distance-to-water | 2, 326 | 2.87 | 0.0584 | I < II |
| Straightness index SI | Season | 2, 326 | 2.01 | 0.1361 | |
| | Distance-to-water | 2, 326 | 0.87 | 0.4179 | |
| Fractal dimension <i>D</i> | Season | 2, 326 | 0.38 | 0.6854 | |
| | Distance-to-water | 2, 326 | 2.73 | 0.0665 | I > II & III |

The last column provides qualitative information on the results, with symbols indicating significance between classes at the *P* level of 0.05. I, II and III represent the 3 classes of distance to water: 0–2 km (close), 2–6 km (intermediate), and 6–10 km (far), respectively. Early, late and dry represent the early dry season, the late dry season and the wet season, respectively. See Fig. 5 for the graphical representation of the results. The interaction is represented when the effect was significant at the *P* level 0.05 only

the early dry season. One possible explanation resides in the fact that even though lions are opportunistic predators seasonal shifts in prey selection appear to occur in seasonal environments (Owen-Smith 2008). In HNP, it is likely that lions mainly rely on greater kudu (*Tragelaphus strepsiceros*) in the early dry

season (*unpublished data*), and lioness home range size is influenced by the abundance of kudu in the early dry season (Loveridge et al. 2009). Kudus are browsers and most of the park is covered by woodland and bushland (Rogers 1993), and they are less water-dependent than other prey species (often

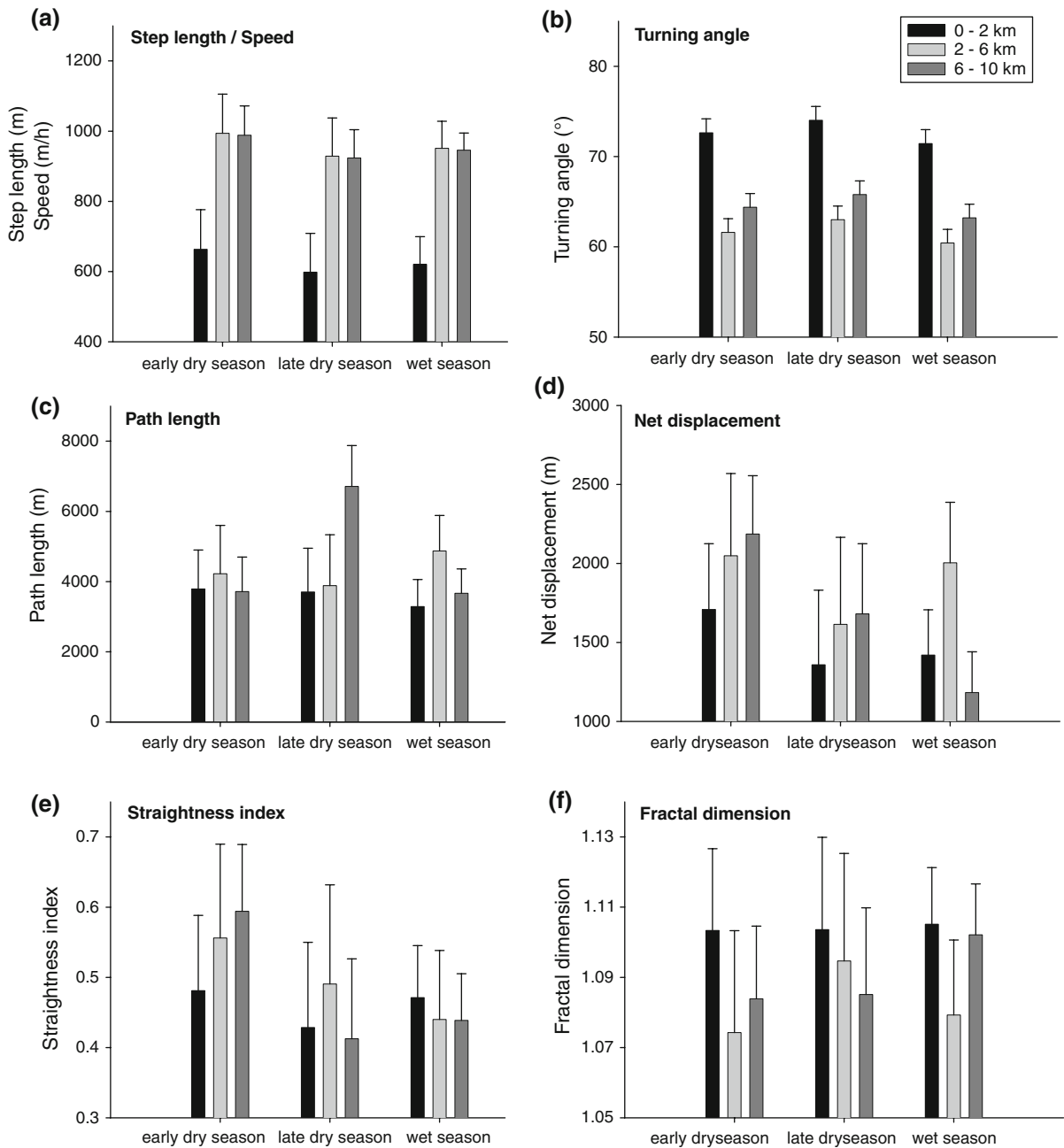


Fig. 5 Representation of male African lions night path movement characteristics (estimate + SE) for each distance-to-water class and each season in Hwange National Park, Zimbabwe. The following night path characteristics are

displayed: **a** step length (it also equals speed since step length is the distance travelled during 1 h), **b** turning angle, **c** path length, **d** net displacement, **e** straightness index, and **f** fractal dimension

grazers). They are consequently less predictably distributed than other prey species.

In summary, our results are in line with a scenario whereby, throughout the year, lions (1) use several waterholes, (2) spend most of their time in areas

surrounding these waterholes, (3) adopt area-restricted search behaviour in these areas, and (4) travel quickly using straight lines when they move from one waterhole area to another, hence spending the least possible time far from waterholes where

potential prey are scarce. In arid and semi-arid savannas, large herbivores are more abundant in the vicinity of waterholes (Redfern et al. 2003; Valeix et al. 2009) where they have to go and drink regularly, and are accessible and vulnerable to predation by lions in the vegetation surrounding these water sources (Hopcraft et al. 2005). Hence, it is very likely that the underlying mechanism of the patterns revealed here is that lions spend more time in the vicinity of waterholes and explore these areas thoroughly to maximise their encounter rate with potential prey in areas where prey are relatively more abundant and accessible. Our study corroborates previous findings on large free-ranging predators in marine ecosystems (e.g. Pinaud and Weimerskirch 2005; Bailey and Thompson 2006) which demonstrated that predators use area-restricted search behaviour in areas of high resource abundance. Our results further provide an illustration of how key habitat features (e.g. waterholes in this study), which determine the dispersion of prey, may have a determining influence on predator spatial ecology and movement patterns. Suitable habitats are dictated by the dispersion of these key habitat features. Additionally, predators move differently when they are close to or far from these key habitat features.

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